



# Indirect host-mediated effects of an exotic phloem-sap feeder on a native defoliator of balsam fir



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## ABSTRACT

Since its introduction from Europe, balsam woolly adelgid [*Adelges piceae* (Ratzeburg) (Hemiptera: Adelgidae)], a phloem-sap feeder, has spread throughout the balsam fir [*Abies balsamea* L. (Mill.)] forests of eastern Canada. Trees under *A. piceae* attack develop “gout” and differ from unattacked trees in physiology, morphology, growth, and chemistry. The native and eruptive eastern spruce budworm [*Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae)] also attacks fir, causing severe defoliation during outbreaks. While balsam woolly adelgid and budworm feed at different times and on different host tissues, such spatiotemporally separated herbivores may still interact via host-mediated indirect effects. We examined the relationship between gout and the performance of developing budworm larvae in balsam fir dominated stands in western Newfoundland. We tested for adelgid–budworm interactions in unthinned and precommercially-thinned (~20 years past) stands, because the host’s growing condition can affect foliage composition and herbivore performance.

Budworm attained lower pupal weight when reared on trees with high levels of gout. In unthinned stands moderate gout reduced budworm survivorship, but there was no such effect in thinned stands. Gout did not affect budworm sex ratio. Although our data are consistent with interactions mediated by foliage quality (rather than quantity), and although budworm survivorship was associated with several aspects of foliage chemistry (Mg and N, positive; monoterpenes, negative), we were unable to identify specific host quality changes underlying the adelgid–budworm interaction. Our study demonstrates that *A. piceae* attack is an important factor influencing budworm performance, and it should be considered when analyzing budworm population dynamics and when developing management protocols for forests impacted by *A. piceae* attack.

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## 1. Introduction

Spatially or temporally separated herbivores exploiting shared hosts may interact indirectly when they alter the quantity or quality of available host tissues. Such interactions can be either facilitative or competitive (e.g., Denno et al., 1995; Karban and Baldwin, 1997; Heard and Buchanan, 1998; Ohgushi, 2005; Kaplan and Denno, 2007; Tabuchi et al., 2011), and the interacting herbivores can have more-than- or less-than-additive effects on their hosts (Morris et al., 2007). Host-plant mediated competition is likely when one herbivorous species reduces the performance

of another by inducing changes in plant physiology, phenology, morphology, defensive chemistry, or nutritional value (Karbon and Baldwin, 1997). Such indirect competition has been observed more frequently in systems that include introduced species than in all-native systems (Denno et al., 1995), perhaps because herbivore impacts are expected to be more severe in evolutionarily novel associations (Heard and Kitts, 2012). As introduced species become established and spread globally, host-plant mediated interactions between herbivores may become increasingly important in structuring communities (Masters and Brown, 1997) and in shaping best management practices. In a forestry context, examples may include interactions between hemlock woolly adelgid and elongate hemlock scale on hemlock (invasive/invasive; Preisser and Elkinton, 2008), between brown spruce longhorn beetle and spruce budworm on spruce (invasive/native; S.B. Heard et al., unpubl. data), and between balsam woolly adelgid and

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spruce budworm on balsam fir (invasive/native, and the topic of this paper).

In Atlantic Canada, most balsam fir [*Abies balsamea* L. (Mill.)] stands now show signs of feeding by the exotic balsam woolly adelgid, *Adelges piceae* (Ratzeburg) (Hemiptera: Adelgidae), which was introduced to eastern North America approximately 100 years ago (Kotinsky, 1916; Quiring et al., 2008). While even large populations of *A. piceae* need not greatly impact their native host, European silver fir [*Abies alba* (Mill.)] (Balch, 1952; Ragenovich and Mitchell, 2006), North American *Abies* spp. show a hypersensitive reaction when fed upon by this adelgid. The reaction includes stunting of terminal shoot growth and abnormal swelling of buds and nodes (Balch, 1952), which have led to description of the condition as “gout”. These visible effects are accompanied by exaggerated cell growth in the bark and cambium, inhibition of bud production, and reduced photosynthetic capacity (Balch, 1952). Thickening of cell walls and reductions in tracheid pit apertures disrupt water conduction to the crown of the tree (Balch, 1952; Ragenovich and Mitchell, 2006). Severe and continued gout can cause branch, crown and even tree mortality (Balch, 1952), but shorter-term effects are felt as well: *A. piceae* attack alters branch growth and chemistry of one-to-four-year-old balsam fir foliage (Grégoire et al., 2014). *A. piceae* may well have other impacts on its host trees, which would be correlated with the occurrence of gout, and therefore we emphasize that, in what follows, we use gout as a proxy for *A. piceae* attack history and impacts more broadly.

The current ubiquity of *A. piceae* in the fir stands of eastern Canada and its marked influence on the morphology and physiology of fir trees suggest that it could have important effects on the performance of other herbivores with which it shares hosts. Balsam fir is a primary host for many native herbivores, among which the eastern spruce budworm (*Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae); henceforth, just “budworm”) is of particular importance to ecology, harvesting, and management of eastern Canadian forests. Budworm is an oligophagous, eruptive herbivore common in eastern North America (Blais, 1983; Royama, 1984). It causes widespread defoliation, tree mortality and economic losses during outbreaks (e.g., Hennigar et al., 2011; Zhao et al., 2014). Budworm larvae feed primarily on buds and current-year foliage of balsam fir and white spruce [*Picea glauca* (Moench.) Voss] but also cause measurable defoliation in red [*P. rubens* (Sarg.)] and black [*P. mariana* (Mill.)] spruce (Hennigar et al., 2008). In general, past studies of budworm dynamics (Morris, 1963; Royama, 1984; Gray, 2008), impact (MacLean and Ostaff, 1989; Piene, 1989; Nealis and Régnière, 2004; Campbell et al., 2008), and management (Crook et al., 1979; Bauce, 1996; Hennigar et al., 2011) have been carried out in apparently *A. piceae*-free stands. As a result, little is known of how *A. piceae* will interact with budworm and whether *A. piceae* could influence budworm outbreak dynamics.

Interplant competition can affect foliage quality, which can then influence herbivore performance (e.g., Awmack and Leather, 2002; Lamontagne et al., 2002; Kumbaşlı et al., 2011). In managed forest landscapes, major reductions in competition between trees are achieved by the silvicultural practice of precommercial thinning (hereafter, just “thinning”) to increase forest yield (e.g., Koga et al., 2002). Thinning of balsam fir [*Abies balsamea* (L.) Mill.] can either increase (Kumbaşlı et al., 2011) or decrease (Bauce, 1996) the performance of insect defoliators. Whether thinning might also influence interactions between herbivore species attacking different tissues remains unknown; however, we previously demonstrated that both thinning and *A. piceae* gout affect bud and shoot growth in fir (Grégoire et al., 2014), and hence they may have interactive effects on budworm. We carried out field experiments to test the hypothesis that *A. piceae* gout would reduce budworm performance on fir, perhaps by reducing branch

growth and altering foliage chemistry. We also tested the hypothesis that thinning would modify the adelgid–budworm interaction.

## 2. Materials and methods

### 2.1. Effects of gout, budworm density, and thinning on defoliation and budworm performance

We studied adelgid–budworm interactions in mature balsam fir stands in western Newfoundland, Canada. Stand and tree selection are described in detail in Grégoire et al. (2014). Briefly, stands were dominated by balsam fir and black spruce >40 years old, with scattered white birch (*Betula papyrifera* Marsh.) and a ground cover primarily of mosses. In 2008 and 2009, we selected four pairs of stands based on the presence of *A. piceae* populations and gout damage, and on the absence of significant herbivory by other insects. One stand of each pair had been thinned (in 1986–1989, ~20 years before our study); the other was unthinned. Thinned stands had 6000–8500 stems/ha and mean diameter at breast height of 9.6–12.2 cm, while unthinned stands had 10,500–43,000 stems/ha and mean dbh 5.8–8.3 cm. In each stand we chose five otherwise healthy dominant or co-dominant balsam fir trees in each of three gout level classes. “Low” gout trees had no visible trace of swollen nodes; “medium” gout trees had 20–40% of axial nodes and <10% of lateral nodes swollen; and “high” gout trees had >70% of axial nodes and >40% of lateral nodes swollen. We excluded any tree that showed symptoms of herbivory by insects other than *A. piceae*, or had produced cones in the previous or current year (because cone production can reduce resource allocation to foliage; e.g., Morris, 1951).

We chose five mid-crown branches on each tree and randomly assigned each to one of five target budworm densities: 0, 0.25, 0.50, 0.75, and 1 budworm larva per bud. These densities are commonly reached during outbreaks. The zero-budworm branches were used only to confirm that such branches did not suffer defoliation, and we do not discuss them further. We used budworm larvae obtained from the Insect Production Services of the Canadian Forest Service in Sault Ste. Marie, Ontario because we observed no wild larvae at our study sites. We transferred second-instar larvae onto current-year shoots of the study branches on 1 cm<sup>2</sup> pieces of cheesecloth, prior to budburst and approximately 24 h before larvae emerged from their hibernacula. We placed a 1 m<sup>2</sup> sleeve cage of fine mesh over each branch, as in Quiring and McKinnon (1999), to prevent larvae from dispersing and to protect them from natural enemies.

Once >80% of larvae had pupated (mid-July), we cut the branches and transported them, in their sleeve cages, to the laboratory. When pupae developed visible eyespots, we weighed, counted, and sexed them (Jennings and Houseweart, 1978). We estimated defoliation of current-year shoots for each branch using classes of 0%, 1–10%, 11–20%, 21–40%, 41–60%, 61–80%, 81–99%, and 100% defoliation (Parsons et al., 2005). Shoots ≥ 1 year old did not suffer significant defoliation.

We analyzed five dependent variables: defoliation, and four measures of budworm performance (larval survivorship, sex ratio, male pupal weight, and female pupal weight). We analyzed pupal weight separately by sex because budworm show strong sexual size dimorphism. Because we were not interested in possible variation among trees in susceptibility, we averaged each performance measure across the five replicate trees in each stand to improve fit to distributional assumptions. Because our design was complex, and because we were primarily interested in how defoliation and budworm performance responded to gout and budworm density, we conducted statistical analysis in two main steps.

First, we asked whether thinning influenced the effects of gout (low, medium, high, treated as categorical) and budworm density (0.25–1.0 larva/bud, treated as continuous) on defoliation and budworm performance (that is, we tested for thinning  $\times$  gout and thinning  $\times$  density interactions). Because thinning was applied at the stand level, and because our thinned and unthinned stands were paired by location, for each dependent variable we calculated contrasts (thinned minus unthinned in each stand pair) for each treatment combination in each year. A significant dependence of this contrast on a treatment would indicate a thinning  $\times$  treatment interaction. At the same time, we asked whether variation associated with stand pair and year influenced our assessment of the fixed effects we wanted to study, using mixed-model analysis of variance via the lme function of package nmle (Pinheiro et al., 2014) in R version 3.1.1 (R Core Team, 2014). In this modeling, we used the Akaike Information Criterion to judge whether models including stand pair and/or year as random effects outperformed a simpler fixed-effects model considering only gout level and budworm density. For larval survivorship, sex ratio, male pupal weight, and defoliation, no model including random effects was appreciably better than the fixed-effects-only model (all  $\Delta$ AIC < 0.85). For female pupal weight, a model that included stand pair but not year was distinctly better than the fixed-effects-only model ( $\Delta$ AIC = 11.2), but interpretation of the fixed effects was identical in the two models. Therefore, in all cases we tested hypotheses about gout and budworm density in fixed-effects analyses using the gls function of package nmle. We first tested for significance of the gout  $\times$  budworm density interaction (using the drop1 command), and as it was never close to significance (all  $P > 0.75$ ) we pooled its variance with the error. This left us with models, for each dependent variable, of the thinned-unthinned contrast depending only on gout level and budworm density. Significant effects in such models would indicate that thinning interacts with gout or budworm density to influence defoliation or budworm performance. We inspected residual plots associated with all models to check for trends or heteroscedasticity, but found none.

Second, we tested for simple effects of gout and budworm density on defoliation and budworm performance. For dependent variables where our analyses revealed interactions of thinning with gout or budworm density (last section; this was true for larval survivorship and sex ratio), we ran separate analyses for thinned and unthinned stands. We used fixed-effects analysis of variance to test dependence of each dependent variable on gout level and budworm density, using the gls function and the drop1 command to provide tests of the gout  $\times$  density interaction and of each main effect. Larval survivorship, sex ratio, and defoliation were proportion data and we therefore subjected them to logit transformation before analysis; because our data included values of 0 and 1, we used the “empirical logit”,  $\log[(y + \varepsilon)/(1 - y + \varepsilon)]$ , where  $\varepsilon$  is the smallest nonzero proportion observed (Warton and Hui, 2011). In each case the gout  $\times$  density interaction was far from significance (all  $P > 0.18$ ), so we pooled its variance with the error. For variables without interactions involving thinning, we included both thinning treatments in a single analysis of variance. Here we began with a model including a term testing for an effect of thinning, but since this term never approached significance (all  $P > 0.17$ ) we dropped it and proceeded with two-factor analyses (gout and budworm density) as above. Again no interaction term approached significance (all  $P > 0.51$ ) and we pooled interaction variance with the error; and again we inspected residual plots to check for trends or heteroscedasticity, but found none.

## 2.2. Associating foliage chemistry with budworm performance

We measured chemistry of current-year balsam fir foliage in 2009, collecting foliage samples from branches with low, medium,

and high levels of *A. piceae* gout when most budworm larvae were 3rd instars, and then again when most larvae were 5th instars. To ensure that effects of *A. piceae* attack were not confounded with changes in foliage chemistry induced by budworm feeding, we sampled different trees from those used for budworm sleeve-caging. Full details of sampling and chemical analysis are reported in Grégoire et al. (2014).

We evaluated the influence of foliar chemistry on budworm larval performance (i.e., survival, sex ratio, and pupal weight) using canonical correlation analysis. We carried out an initial correlation analysis and dropped any variables violating the multivariate assumption of multicollinearity. We further reduced the dataset by eliminating redundant and nonresponsive variables (Tabachnick and Fidell, 2001). After this variable selection, we used principal components analysis to reduce dimensionality in the subsequent canonical correlation analysis. We standardized data to a mean of zero and a standard deviation of one prior to analysis and used a cut-off correlation of 0.3 (Tabachnick and Fidell, 2001). All multivariate assumptions were met.

## 3. Results

### 3.1. Effects of gout, budworm density, and thinning on defoliation and budworm performance

Defoliation responded to treatments similarly in thinned and unthinned stands (Table 1), increasing with budworm density (Fig. 1) but being unaffected by gout level or thinning (Table 2). Larval survivorship responded differently to treatments in thinned and unthinned stands (both thinning  $\times$  gout and thinning  $\times$  density interactions significant; Table 1). In unthinned stands, survivorship decreased strongly with budworm density, while a similar trend in thinned stands was weak and non-significant (Table 2, Fig. 2). In unthinned stands, survivorship was lowest on trees with medium gout (Fig. 3, left), but in thinned stands gout had no effect on survivorship (Table 2) and if anything the survivorship-gout pattern was reversed (Fig. 3, right).

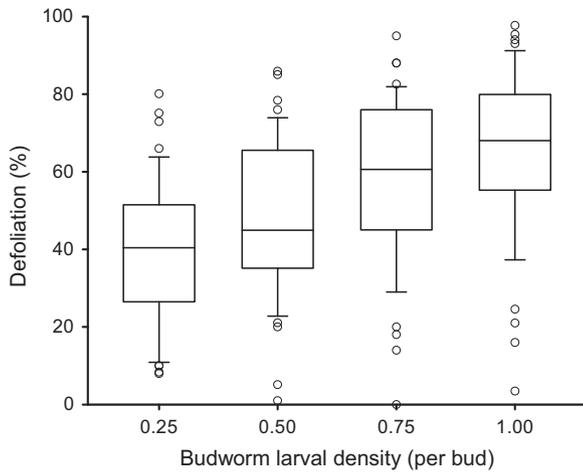
Sex ratio appeared to respond differently to gout, although not to larval density, in thinned and unthinned stands (Table 1). However, when we broke the analysis down by thinning treatment, neither gout nor budworm density had a significant effect on sex ratio in either stand type (Table 2). All sex ratios were close to 1:1 (overall average 47% female).

Male and female pupal weights responded to treatments similarly in thinned and unthinned stands (Table 1). Females were heavier than males (average 0.056 versus 0.041 g), as expected. Pupal weight decreased with increasing larval density in both sexes (Table 2), although the decrease was steeper for females than males (Fig. 4). Pupal weight also decreased with increasing gout

**Table 1**

Tests for defoliation and four performance variables of thinning  $\times$  gout and thinning  $\times$  budworm density interactions. *G* is the likelihood ratio test statistic; *P* values in bold are significant ( $P < 0.05$ ).

Dependent variable	Interaction	df	<i>G</i>	<i>P</i>
Defoliation	Thinning $\times$ Budworm density	1	0.04	0.84
	Thinning $\times$ Gout	2	1.10	0.58
Larval survivorship	Thinning $\times$ Budworm density	1	6.52	<b>0.011</b>
	Thinning $\times$ Gout	2	11.6	<b>0.0031</b>
Sex ratio	Thinning $\times$ Budworm density	1	1.77	0.18
	Thinning $\times$ Gout	2	6.65	<b>0.036</b>
Male pupal weight	Thinning $\times$ Budworm density	1	0.46	0.50
	Thinning $\times$ Gout	2	1.68	0.43
Female pupal weight	Thinning $\times$ Budworm density	1	0.37	0.54
	Thinning $\times$ Gout	2	4.66	0.059



**Fig. 1.** Effect of budworm density on defoliation. Boxes show 25th and 75th percentiles, whiskers 10th and 90th. No other treatment significantly influenced defoliation.

in both sexes (Table 2). Male pupae were smaller at either medium or high gout (compared to the low gout treatment), while female pupae were smaller only at high gout (Fig. 5). There was no effect of thinning on pupal weight in either sex.

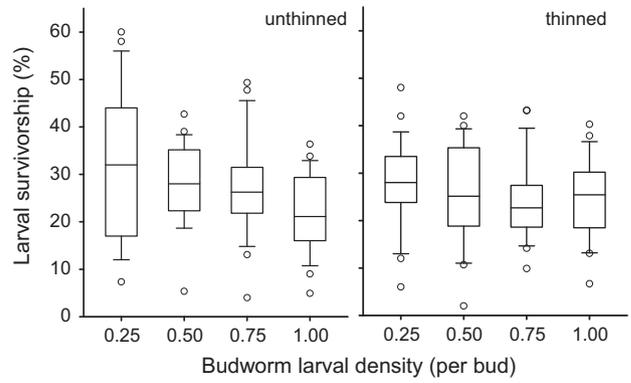
3.2. Associating foliage chemistry with budworm performance

Canonical correlation analysis revealed a significant association between the chemistry of balsam fir foliage and both budworm larval survival and female pupal weight (Wilks'  $\lambda = 0.4476$ ,  $F_{8,36} = 2.23$ ,  $P = 0.048$ ) (Table 3). Four distinct principal components were obtained and used in the canonical correlation. The first pair of canonical variates indicated that increasing foliar contents of  $Mg_{(Early \& Late)}$  (first principal component; 0.64) and decreasing foliar contents of  $N_{(Early)}$  and  $monoterpenes_{(Late)}$  (third principal component;  $-0.71$ ) were associated with greater budworm survivorship (0.99) and female pupal weight (0.35). The effect of the second pair of canonical variates was not significant ( $F_{3,19} = 0.69$ ,  $P = 0.569$ ).

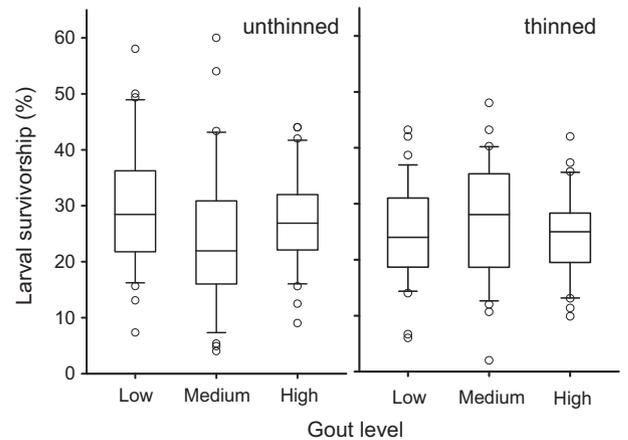
4. Discussion

4.1. Thinning

Thinning had no effect on defoliation or on budworm pupal weights. While thinning appeared to interact with gout to influ-



**Fig. 2.** Effect of budworm density on larval survivorship in unthinned and thinned stands. Effects of density were independent of those of gout (Fig. 3).

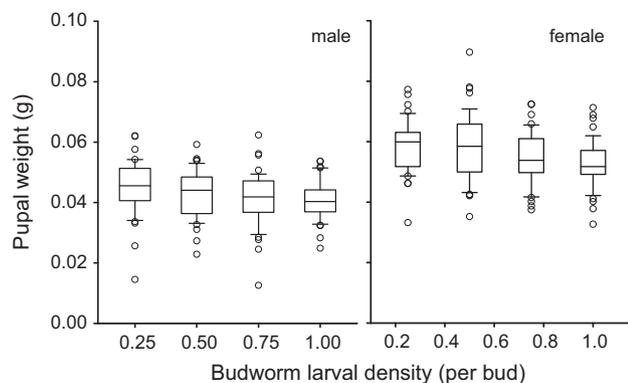


**Fig. 3.** Effect of gout level on larval survivorship in unthinned and thinned stands. Effects of gout were independent of those of budworm density (Fig. 2).

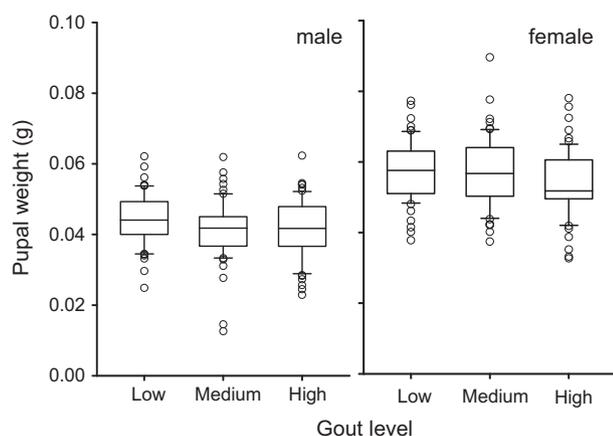
ence sex ratio, its effect was extremely subtle: we could detect no treatment effects on sex ratio when unthinned and thinned stands were analyzed separately, and all sex ratios were close to 1:1 (as expected for resident budworm populations; Rhoads and Heard, 2015). Thinning did interact with both budworm density and gout to influence budworm survivorship: survivorship declined with budworm density and with gout in unthinned stands, but not (significantly) in thinned ones. These modest effects of thinning overall are consistent with results of Grégoire

**Table 2**  
Tests for gout and budworm density effects on defoliation and four budworm performance variables. *G* is the likelihood ratio test statistic; *P* values in bold are significant ( $P < 0.05$ ). Where thinning is noted as "pooled", a test for a main effect of thinning was far from significant (all  $P > 0.17$ ) and was removed from the model.

Dependent variable	Thinning	Treatment	df	<i>G</i>	<i>P</i>
Defoliation	Pooled	Budworm density	1	33.5	<b>&lt;0.0001</b>
		Gout	2	0.43	0.80
Larval survivorship	Unthinned	Budworm density	1	8.51	<b>0.0035</b>
		Gout	2	6.14	<b>0.046</b>
	Thinned	Budworm density	1	0.58	0.45
		Gout	2	0.84	0.66
Sex ratio	Unthinned	Budworm density	1	1.71	0.19
		Gout	2	1.33	0.51
	Thinned	Budworm density	1	0.13	0.72
		Gout	2	3.90	0.14
Male pupal weight	Pooled	Budworm density	1	7.68	<b>0.0056</b>
		Gout	2	6.43	<b>0.040</b>
Female pupal weight	Pooled	Budworm density	1	13.67	<b>0.00021</b>
		Gout	2	6.70	<b>0.035</b>



**Fig. 4.** Effects of budworm density on male and female pupal weight. Effects of density were independent of those of gout (Fig. 5).



**Fig. 5.** Effects of gout level on male and female pupal weight. Effects of gout were independent of those of budworm density (Fig. 4).

**Table 3**

Summary of canonical correlation analysis between *C. fumiferana* performance (larval survival and female pupal weight) and the chemistry of current-year balsam fir foliage sampled when most *C. fumiferana* larvae were early (third) or late (fifth) instars. The first canonical correlation was 0.71 ( $F_{8,36} = 2.23$ ,  $P = 0.048$ ).

First canonical variate	Correlation
<i>C. fumiferana</i> performance	
Larval survival	0.999
Female pupal weight	0.35
Percent of variance	0.54
Redundancy	0.28
Foliar chemistry	
PC1: $Mg_{(Early)}$ and $Mg_{(Late)}$	0.64
PC2: $-\log$ soluble sugars $_{(Early)}$ , $\log Ca_{(Early)}$ and, $Ca_{(Late)}$	0.27
PC3: $-N_{(Early)}$ and Monoterpenes $_{(Late)}$	-0.71
PC4: Phenolics $_{(Late)}$	-0.12
Proportion of variance	0.25
Redundancy	0.13
Canonical correlation	0.71

et al. (2014), who reported no influence of thinning on tree growth in the same stands. However, they contrast with previous studies that have repeatedly demonstrated positive effects of thinning on tree growth and on tolerance of budworm attack (e.g., Bauce, 1996; Fuentealba and Bauce, 2012) and have therefore suggested thinning as a management tool to reduce the impact of budworm outbreaks (Crook et al., 1979; Bauce, 1996; Hennigar et al., 2011; Fuentealba and Bauce, 2012). We suspect this difference in the

importance of thinning arises because most previous studies have conducted experiments within five years of thinning, whereas our work took place ~20 years after thinning (in stands >40 years old). Our results suggest that the benefits of thinning for budworm management in balsam fir stands do not persist indefinitely. This is consistent with the suspected mechanisms for effects on thinning on forest herbivores (Fettig et al., 2007), most of which should attenuate as trees in thinned stands grow and the canopy recloses.

#### 4.2. Budworm density

High budworm densities led to high defoliation, low larval survivorship, and low pupal weight of survivors – all as expected. At our highest budworm density (1 larva/bud), defoliation of current-year shoots was about 66% on average and over 80% on 26% of branches. These levels of defoliation would be common during a budworm outbreak. Because available foliage was clearly depleted at high budworm density, the effects of density on performance in our data likely arose, at least in part, by exploitative competition between budworm larvae for limited quantities of suitable foliage.

#### 4.3. Gout and foliage chemistry

High levels of attack by balsam woolly adelgid (identified in our study by moderate or high levels of gout) impaired performance of budworm larvae. In unthinned stands, budworm survivorship was lower on moderately gouted trees, although no reduction was apparent on highly gouted trees. More importantly, in both stand types, pupal weight of survivors was lower on gouted trees. Male pupal weights decreased when larvae were reared on both medium and highly gouted trees, while female pupal weights decreased markedly only on highly gouted trees. These results suggest that male budworm may be more sensitive to gout-related changes in the quality of foliage than are females.

Adult budworm feed only on carbohydrates and water and must rely on larval stores for the majority of their resources (Boggs and Freeman, 2005). As a result, fecundity is directly related to pupal size (Lorimer and Bauer, 1983; but see Robison et al., 1998). The impact we observed of gout on female pupal weight, therefore, is likely to correspond to reduced fitness and reduced growth rate of budworm populations. Reduced pupal weight in males may also impact fitness: smaller males have lower mating success (Delisle and Hardy, 1997), perhaps because they cannot maintain the flight activity necessary to locate mates (Silk and Kuenen, 1988; Rhains and Brodersen, 2012). The higher sensitivity of male versus female pupal mass to gout may reflect a tradeoff between optimal body size and emergence time that improves male mating success under stressful conditions by ensuring males emerge before females, as in other insects (Teder and Tammaru, 2005; Gibbs et al., 2006).

Our data suggest that the impact of gout on budworm performance reflects decreased quality, rather than quantity, of available foliage. Budworm density did not interact with gout level to influence defoliation or any performance measure, as we might have expected had foliage quantity been the important mechanism for gout effects. Shoot elongation was reduced on gouted branches (Grégoire et al., 2014), suggesting that these branches were likely to possess lower quality resources than ungouted branches. While bud production was also reduced on gouted branches (Grégoire et al., 2014), our budworm density treatments were defined on a per-bud basis and thus remove effects of bud production. Had we stocked budworm per branch, rather than per bud, we likely would have found additional effects of gout based on reduction in foliage quantity. Such quantity effects might become important in a natural outbreak as budworm densities increase past the abil-

ity of females to locate underexploited branches for their offspring. Whether female budworm avoid gouted branches during oviposition is currently unknown, although we have detected such avoidance in another common defoliator of balsam fir (balsam fir sawfly, *Neodiprion abietis*; Grégoire et al. unpubl.).

While our experiments were not designed to evaluate the interactive effects of *A. piceae* and budworm attack on growth and survival of balsam fir, the possibility of such effects is clearly an important issue for the future of balsam fir in North American forests. Reductions in budworm performance associated with *A. piceae* attack might suggest a less-than-additive impact of the two herbivores. However, greater-than-additive impacts are also possible if gout-stressed trees are less tolerant of additional herbivore impact. Either less-than-additive or greater-than-additive impacts can arise when two herbivores exploit a common host (Morris et al., 2007), but how impacts of *A. piceae* and budworm combine remains unknown.

Altered foliage chemistry is a potential mechanism by which *A. piceae* might influence other herbivores, including budworm. Indeed, our canonical correlation analysis suggests that budworm survivorship, and to a lesser extent female pupal weight, are positively associated with foliar Mg and N and negatively associated with foliar monoterpene content. Concentrations of N have previously been related to budworm pupal weight (Mattson et al., 1991), and although Clancy and King (1993) reported a negative effect of Mg on the performance of western spruce budworm (*C. occidentalis*), the lowest concentration they tested was well above the average concentration measured in our study. Trees with high levels of monoterpenes are more resistant to budworm attack (e.g., Chen et al., 2002; Fuentealba and Bauce, 2012) and budworm larvae fed monoterpene-rich foliage pupate at lower weight (Mattson et al., 1991; and for *C. occidentalis*, Redak and Cates, 1984; Cates et al., 1987). Unexpectedly, though, in our stands decreases in branch growth with gout were not accompanied by changes in measured chemistry of current-year foliage (Grégoire et al., 2014). Consequently, even though highly gouted trees were nutritionally inferior for budworm, and even though we found significant (indirect) correlations between budworm performance and foliage chemistry, we cannot connect the reduced size of budworm reared on gouted trees to variation in specific nutrients or secondary chemicals. More work is thus needed to determine the mechanism of gout effects on budworm performance. This could involve experiments directly manipulating foliage chemistry of both gouted and ungouted trees (perhaps by fertilization; e.g., Timmer and Stone, 1978), as well as studies measuring variation in additional aspects of foliage chemistry or other characteristics of balsam fir foliage. Another interesting possibility is that *A. piceae* attack might interact with budworm feeding to induce foliage-quality changes more severe, or different, than those induced by *A. piceae* attack alone. Such interactive effects could be particularly important in the later phases of future budworm outbreaks, when many trees will have experienced attack by both herbivores over multiple years.

## 5. Conclusions

We have shown that larval development of balsam fir's most damaging native defoliator (eastern spruce budworm) is significantly impaired on heavily gouted trees – that is, those suffering high levels of damage by balsam woolly adelgid. The effect of gout on budworm development appears to be mediated by foliage quality, although we were not able to identify a specific mechanism in foliage chemistry. Reductions in budworm larval performance are likely to compromise adult mating success and fecundity, and therefore reduce population growth rates. The relationship

between gout and budworm performance should therefore be an important consideration in the analysis of budworm population dynamics and in the development of management protocols when budworm outbreaks build in areas with high densities of *A. piceae*. More broadly, it is likely that other invasive forest pests will have similar impacts on the native herbivores they interact with, because (like balsam woolly adelgid) many invasives have severe impacts on their newly adopted hosts.

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